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The Responses of Avena Sativa To Consecutive Stimuli

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THE RESPONSES OF AVENA SATIVA TO CONSECUTIVE STIMULI

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THE RESPONSES OF AVENA SATIVA TO CONSECUTIVE STIMULI.

It is a well known fact that shoots of young seedlings respond in a negative manner to the stimulus of gravity. This is demonstrated conclusively by the fact that the shoots of plants show an upward curvature of the tips when placed horizontally in the dark for an hour. The period of time elapsing between the horizontal placing, which allows the geotropic stimulus to act, and the first bending of the tip is called the reaction period. Not all of this period is necessary to cause response, however. It is divided into two parts: (1) the presentation period, or the shortest time of stimulation necessary to produce a curvature, and (2) the latent period, or that time between the presentation period and the time at which the response manifests itself. The former period is needed for the reception of the stimulus, and the latter for the growth processes to which curvature is due.

Czapek ('98,p.187) investigated the relation existing between the length of the reaction period and the period of stimulation and concluded that the reaction time decreases with the lengthening of the presentation period, at first slowly and then rapidly until a minimum is reached. On the other hand Bach ('07, p.79) states that there is little difference in the length of the reaction period between those which are stimulated during only the presentation period and those which are left in a

horizontal position until curvature begins, and makes the following statement: "Durch Einwirkung des geotropischen Reizes während der Dauer der Präsentationszeit wird also schon das Minimum der Reaktionszeit erreicht".

Fitting's investigations of 1905 (p.393) have shown that a movement may be induced in a plant due to the summation of intermittent stimuli, when each stimulus is of much shorter duration than the presentation period and that geotropic curvature takes place even when the intervals are ten times as long as the periods during which the stimulus is applied.

Czapek in 1895 (p.343) and again in 1898 (p.185) gives the presentation period for Avena sativa as 15 minutes and the reaction period as 60 to 70 minutes at 18° C, and states that between 15° and 35° C. there is no apparent alteration in the length of these periods. Bach ('07, p.71) found that the lengths of the presentation and reaction periods are closely related to the degrees of temperature lying between 40° and 35° C. and that this relation is similar for both of the periods. With a rise of temperature from 14° C. there is a distinct shortening of the periods until they reach their minimum at about 30° C. Above this temperature the lengths of the periods increase.

There can be no doubt that the presence of impure air in the laboratory greatly alters the responses of the plants. Richter ('05, p.314) and Molisch ('06, p.8) found that the sensibility of plants to geotropic stimulus is greatly decreased and often

entirely overcome through the influence of gaseous impurities.

If a plant be so placed that its shoot grows vertically upward no curvature takes place. If, however, the shoot be placed at an inclination to the vertical so that the line of direction of gravity makes an angle with it, a curvature results, owing to the fact that on the lower side growth is accelerated while on the upper side it is retarded. The influence of gravity has the greater effect the more nearly the stem approaches the horizontal. In that position gravity has its maximum mechanical effect and when the plant is still farther turned the effect is again diminished until finally in the inverted position it reaches zero. Fitting ('05, p.326) states: "dass die Horizontale die optimale Reizlage ist".

When seedlings are slowly and steadily rotated in a horizontal position on a klinostat, no curvature takes place. The revolutions, however, must be so regulated that the position of the plants is continually altered before the inductive stimulating action of gravity is expressed on any one side. Czapek ('98, p.188) advanced the theory that the length of time consumed in one revolution of the wheel must not be more than four times the presentation period of the plants. He supposes, for the purpose of demonstration, that, in a single rotation the plants occupy four positions, corresponding to the quadrants of the circle. They must pass through each quadrant in a space of time shorter than the presentation period in order that the plants may not receive in any one position sufficient stimulation to produce curvature. If the pot is

revolved too rapidly centrifugal force arises and to this force the shoots respond in a negative manner, turning their tips toward the center of the pot. Czapek ('98, p. 192) found that plants respond to centrifugal force in the same way as to gravity, and that a curvature takes place in six hours when the force is equal to only one one-thousandth of g. On the other hand, when the force is increased to 38 times the value of g. a response is obtained in 45 minutes.

It is still a debatable question as to whether plants are really geotropically stimulated when placed on the klinostat, or whether the individual stimuli acting upon the different sides of the shoots neutralize each other. Fitting's investigations of 1905 which were spoken of above, tend to prove the correctness of the latter theory, namely, that the klinostat does not eliminate geotropic stimulation, but merely prevents curvature from such stimulation.

Vöchting (1882) was the first to show that, when a shoot which has been curved geotropically, is removed from the unilateral influence of gravity by being placed on a klinostat, an attempt is made by the plant to compensate this curvature. It gradually straightens, due to the fact that the concave side whose growth has been retarded during the curving now elongates more vigorously than the convex side. This internal stimulus, in virtue of which the shoot tends to straighten, Vöchting called rectipetalität. The term autotropism is now more generally applied to all such compensatory reactions.

Closely associated with the study of geotropism has been that of heliotropism, or the response of plants to the stimulus of light. When an etiolated seedling is subjected to the influence of unilateral light a curvature, generally toward the light, takes place within a definite period of time. The entire period of exposure, however, is not necessary to produce the response, for, as with geotropism, a comparatively short presentation period suffices for the reception of the stimulus. The far longer interval of the reaction time is needed for the growth processes to which curvature is due.

Czapek ('95, p.343) gave the heliotropic presentation period for Avena sativa as 15 minutes, or the same as that for geotropism. In a later article ('98, p.185) he states that the heliotropic period is only 7 minutes. This difference is probably due to a variation in the intensity of the light employed. Fröschel's experiments ('08, p.248) show very clearly that the length of the presentation period depends upon the intensity of the light. He worked with Lepidium sativum and showed that the presentation period becomes shorter with an increase in the intensity of light. This he found could be expressed in the formula $Jt = J't'$ when J equals the light intensity and t the period of stimulation.

Wiesner in 1893 and in 1895 and Figder in 1893 had worked with various intensities of light, but had confined themselves to the final extent of curvature obtained and to the determination of the smallest and greatest degrees of intensity to which the plant responds.

The quality of the light also has an effect upon the responses. Wiesner (1878) found that the rays at the limits of the violet and ultra-violet regions are the most active, and that the activity decreases from that point so that, in yellow light, practically no heliotropic curvature takes place. The movements begin again, however, in red light and increase towards the ultra-red.

Another factor governing heliotropic phenomena is the absence or presence of gaseous impurities in the laboratory. Richter ('05, p.330) and Molisch ('06, p.8) show that a certain intensity of light which is too weak to cause curvature in a plant in pure air will cause it in impure air; also, that when the light is so increased as to produce curvature in the pure air, the angle formed in a given time is much smaller than that produced in impure air by the same light.

In nature light and gravity act for the most part simultaneously upon plants and the one stimulus interferes with and not infrequently neutralizes the other. Consequently the effects of one component cannot be studied satisfactorily without the elimination of the other. It is very easy to derive pure geotropic responses by the use of a thoroughly darkened room for all experimentations, but it is much more difficult to obtain pure heliotropic responses. This may be done, however, by the use of a specially devised klinostat on which the potted plant and the light are made to revolve in the same relation to each other. In this way, one side

of the plant is constantly subjected to heliotropic stimulation and at the same time all geotropic curvature is prevented by the rotation. Czapek ('98, p.355) uses such a klinostat and finds that geotropism has no effect upon the time of the entrance of heliotropic curvature, but that the final angle is reached much earlier with the klinostat-plants than with those erect and stationary.

Czapek ('95, p.345) gives the results of experiments with consecutive stimuli of light and gravity. He uses among other plants etiolated seedlings of Avena sativa and he first convinces himself that plants rotated on the klinostat and unilaterally lighted begin their heliotropic curvature at the same time as seedlings laid horizontally in the dark begin their geotropic curvature. The bending progresses in the same way in both cases and the final angle of 90° is reached at the same time.

He then places young seedlings horizontally in the dark at a temperature of 17° to 20° C. for 60 to 70 minutes, or until they show the first trace of response. They are now placed erect and unilaterally lighted in such a way that the side which has been turned downward is now turned toward the light, and thus, the tips bend from the light. The curvature of these plants begins to decrease at the same time as heliotropic reaction begins to show in control plants which have not been previously geotropically stimulated. This takes place in 60 to 70 minutes. When, however, plants which have been previously geotropically curved are placed erect in the dark, there is no decrease in the angles evident at the end of this period, but, on the contrary, the geotropic response has not yet reached its maximum. These results, he thinks,

show that primary geotropic induction has no effect on subsequent heliotropic stimulation.

The case is entirely different, however, when the seedlings are subjected first to unilateral light and then are laid horizontally in the dark with the side, which had been turned toward the light, downward. It is now noticeable that there is a distinct difference between these plants and controls which had not been previously heliotropically stimulated. There is a distinct retardation in the entrance of geotropic curvature in the heliotropically stimulated plants in comparison with control plants which are laid horizontally in the dark at the same time. When the period of lighting is varied and comparisons are made with plants which are used as controls and are placed horizontally in the dark at the different times, there is found to be a distinct increase in the retardation of the geotropic reaction with an increase of the preceding period of lighting. Thus, after a period of 10 minutes of heliotropic stimulation there is a retardation of 15 to 20 minutes, while after 60 minutes of stimulation the delay is 120 minutes. From these results Czapek concludes that the preceding heliotropic induction influences the subsequent responses to the action of gravity.

He also subjects plants to unilateral light until curvature begins and then turns them 180° so that the side which has been turned from the light is now toward it. The angles begin to decrease in those previously stimulated at the same time as the controls first turn toward the light. The same thing is true with

geotropism. When plants which have responded geotropically are turned 180° so that the tips point downward instead of upward, there is a decrease in their angles at the same time as control plants first curve geotropically. This shows that the preceding opposing stimuli do not retard curvature caused by subsequent stimulation.

To my knowledge these experiments have never been repeated, although Czapek's methods of experimentation have been criticised in several points.

In the first place, Czapek makes use of an Argand lamp and unless he employs some method of conveying off the gases from the burning lamp, the results are certainly influenced. Richter, as stated above, found that the presence of gaseous impurities effects the responses to both heliotropic and geotropic stimulation. It decreases a plant's geotropic sensibility and increases the heliotropic sensibility. Jost ('08, p.365) makes the following statement: "Die Versuche von Molisch (1905) und Richter (1906) die diesen Einfluss aufgedeckt haben, machen unseres Erachtens eine völlig neue Untersuchung der Frage nach dem Zusammenwirken von Geotropismus und Heliotropismus, und zwar von Grund aus notwendig".

The intensity of the light must also be considered. Czapek does not state the light intensity used in his experiments, but it must be remembered that, at the time when he did this work, he gave the presentation period for heliotropism and geotropism as of equal length. Later he found the heliotropic period much shorter.

It is manifest that the intensity of light must be determined which will give a presentation period of the same length as that for geotropism. This intensity must then be used throughout the series of experiments in order to make the two stimuli, light and gravity, comparable.

I have undertaken to repeat these experiments, paying particular attention to the purity of the air of the laboratory, to the intensity of the light, to conditions of temperature and with the constant use of the klinostat.

METHODS

The seedlings of Avena sativa were used exclusively in this work. The seeds were soaked between damp filter-papers, in a covered dish for 48 hours, or until the roots were from 5 to 10 mm. in length. They were then planted in straight rows in damp sand, about 12 seeds to a pot. The pots were placed on a sand bed and covered with common flower pots the holes of which had been tightly corked. By sinking these into the sand the entrance of light around the lower edge was prevented.

As a rule the plants were sufficiently large to be used in 48 hours after the time of planting. This, however, was not always the case for, unfortunately, an entirely even temperature could not be maintained in the greenhouse and often 72 hours was necessary to obtain seedlings of the size desired. This variation of the temperature no doubt influenced the results of the experiments to a certain extent and may explain some of the irregularities that appear later in this paper.

The seedlings were subjected to light and gravity in a room thoroughly darkened and heated by steam. The temperature varied from day to day from 20° to 27° C. In each case the temperature of the room was noted at the time of experimentation.

In the preliminary work an 8 cp. electric light was used, but since this was of too great an intensity a 4cp. bulb was finally substituted. This was placed in a tin box so constructed that one side was open and over this opening ground glass plates could be slipped to reduce still further the intensity of the light. By varying the number of glass plates, a comparatively fine gradation of the intensity was possible. In order that the heat from the light should in no way effect the actions of the plants they were placed 1 meter distant from it.

The next problem was the construction of a wheel 2 meters in diameter, with the light at some point on the circumference and the pot of plants at the center, the whole wheel turning at the rate of one revolution in 15 minutes. The frame was made of eighth inch gas pipe and the box containing the light was screwed to the end of one of the spokes, a corresponding weight being placed on the opposite side of the wheel. Over the pot of seedlings was inverted a tin cover in which was a slit through which the shoots protruded. This cover prevented the sand from slipping and from falling out of the pot when it was placed horizontally. The pot was then fastened at the center of the wheel with the row of plants horizontal and at right angles to the rays of light. A small electric motor was used to run the machine and by the adjustment of the belts over speed reducers and pulleys the desired rate

of revolution was finally obtained.

EXPERIMENTS

I. Presentation Periods.

The first thing desired was to obtain the exact presentation period for geotropism under the existing conditions of growth, temperature, etc. The plants were placed on a Pfeffer klinostat in a horizontal position and left motionless for a definite period for stimulation. They were then revolved at the rate of one revolution in 15 minutes. In each case the temperature of the laboratory was noted and the length of time elapsing before response.

The following table gives the results: the first column, the length of the period of stimulation; the second, the length of the reaction period; the third, the proportion of plants responding, and the last the temperature of the dark room.

15 min.	45 min.	13 X 13	24° C.
14 "	50 "	10 X 12	24° C.
13 "	50 "	18 X 19	24° C.
12 "	48 "	22 X 25	24° C.
11 "		0 X 10	24° C.
11 "	43 "	26 X 31	27° C.
10 "	45 "	1 X 10	27° C.

Presentation period at 24° = 12 minutes.

Next the presentation period for heli<u>o</u>tropism was obtained. At first an 8 cp. light was used and two distances were tried. The covers were lifted from the pots exposing the plants to the stimulus of light for the desired length of time, and then were quickly replaced. The following results were obtained.

1/2 Meter from light.

1/2 min.	80 min.	7 X 7	23° C.
1 "	65 "	17 X 19	23° C.
2 "	70 "	19 X 20	23° C..
3 "	65 "	7 X 8	23° C.
1/4 "	60 "	4 X 5	24° C.
1/2 "	60 "	8 X 8	24° C.
1 "	60 "	6 X 7	24° C.
1/4 "	60 "	4 X 5	22° C.
1/2 "	60 "	13 X 16	22° C.
1 "	60 "	14 X 17	22° C.
2 "	60 "	7 X 7	22° C.
3 "	60 "	5 X 6	22° C.

It is evident from the above results that the presentation period is not more than 1/4 minute.

1 Meter from light.

1/2 min.	80 min.	6 X 10	23° C.
1 "	60 "	22 X 20	23° C.
2 "	50 "	15 X 18	23° C.
3 "	50 "	7 X 8	23° C.
1/4 "	60 "	7 X 9	24° C.
1/2 "	60 "	11 X 11	24° C.
1 "	60 "	7 X 7	24° C.
1/4 "	60 "	6 X 11	22° C.
1/2 "	60 "	6 X 6	22° C.
1 "	60 "	8 X 10	22° C.
2 "	60 "	6 X 6	22° C.
3 "	60 "	2 X 6	22° C.

This shows that the presentation period is not more than 1/4 minute.

The 8 cp. light was tested and found to be equal to 12.6 Hefnerlamps.

A common candle was then tried with the following results:

1/2 meter from light.

1/2 min.	56 min.	5 X 8	22° C.
1 "	57 "	6 X 8	" "
2 "	56 "	7 X 8	" "
3 "	54 "	9 X 9	" "
4 "	50 "	6 X 6	" "
5 "	50 "	7 X 7	" "

1 meter from light.

1/2 min		0 X 12	22° C.
1 "		0 X 10	" "
2 "	46 min.	5 X 6	" "
3 "	45 "	3 X 6	" "
4 "	44 "	5 X 6	" "
5 "	43 "	6 X 6	" "

It is plain from these results that the presentation period is 1/2 minute when the plants are 1/2 meter from the candle and 2 minutes when they are one meter distant. From these tests it was apparent that the light must be of much less intensity in order to obtain a presentation period equal to that for a geotropic response, namely 12 minutes. A 4 cp. light was then used and before it was placed different numbers of glass plates. With an exposure of 12 minutes the following results were obtained.

6 glass plates	0 X 24 responded
5 " "	6 X 47 "
4 " "	11 X 46 "
3 " "	36 X 54 "
2 " "	8 X 9 "

A majority of the plants, as shown, responded to the intensity of light which was secured by the use of light which

was screened by the use of 3 ground glass plates. In order to make sure that the period of stimulation necessary to produce a response was not shorter than 12 minutes, the following tests were made.

14 min.	40 min.	15 X 17	22° C.
13 "	40 "	24 X 24	" "
12 "	50 "	21 X 22	" "
11 "	50 "	21 X 22	" "
10 "	70 "	1 X 17	" "
9 "		0 X 12	" "

This shows that the presentation is 11 to 12 minutes. The intensity of this light when tested was found to be equal to 1.4 Hefnerlamps.

It was then placed on the specially constructed klinostat described above. The following tests were made in order to assure ourselves that the presentation period was also correct for heliotropism when geotropic response was fully eliminated.

12 min.	60 min.	14 X 14	23° C.
10 "	60 ""	6 X 10	" "
8 "	60 "	0 X 12	" "

It is evident from these results that presentation period is 12 minutes for this intensity of light.

II. Consecutive Stimuli.

a. Stimuli of the same kind but from opposite directions.

Twelve seedlings were subjected to the stimulus of an 8 cp. light, 1 meter distant and in 45 minutes the tips were all turned toward the light. The pots were then turned 180° so that the tips of the plants were pointing from the light. Control

plants, not previously heliotropically stimulated, were exposed at the same time. In another 45 minutes all of the control plants were turned toward the light and the angles of the first plants were decreasing. In 60 minutes 7 out of the 12 plants were turned from the light.

Plants were also laid horizontally in the dark and in 45 minutes 19 out of 19 plants had responded. The pots were turned 180° so that the tips now pointed downward. In 50 minutes 5 out of the 19 plants were almost indifferent and in 70 minutes 15 of them were turned upward.

These results accord with those obtained by Czapek ('95, p. 349) and prove that the response of a plant to subsequent stimulation is not affected by a primary opposing stimulation of the same kind.

b. Heliotropic stimulation after geotropic stimulation.

Seedlings were placed horizontally in the dark for 60 minutes during which time they all responded. They were then placed upright and subjected to the stimulus of an 8 cp. light, 1 meter distance, in such a way that the side was now turned toward the light which had been downward. At the same time plants which had not been previously geotropically stimulated were exposed to the light. In 45 minutes the latter plants were turning toward the light, and those previously geotropically stimulated were straightening. The decrease in their angles took place at the same time and about the same rate as the decrease occurred in the angles of controls which had been geotropically stimulated and then turned 180°.

The same experiment was repeated using the lighted klinostat and at 25° C. The seedlings were placed horizontally in the dark, and in 60 minutes 30 out of 30 plants had responded. They were then fastened to the klinostat in a horizontal position, with the tips turned from the light. In 60 minutes 16 of the plants pointed distinctly toward the light, and the rest of the plants were straightening. Under the same conditions 39 out of 40 plants which had not been previously geotropically stimulated responded to the light stimulus within 60 minutes. These results bear out Czapek's assertion that previous geotropic stimulation does not alter subsequent response to heliotropic stimuli. Czapek, however, asserts ('95, p. 345) that when plants which have responded geotropically are placed erect in the dark, no decrease in their angles will be apparent at the end of 50 to 60 minutes, but that, on the other hand, the response will not be complete at this time. My results lead me to believe that the opposite is correct, namely, that in 50 to 60 minutes there is a distinct upward turning of the tips. Different lengths of exposure were tried and in each case the results were practically the same, as shown in the following table. In the first column are given the various periods of exposure, in the second, the time when each pot was placed erect, and in the other columns the number of plants which were still curved at the times given at the head of the columns.

		10.25	10.35	10.47	11.00	11.15	11.30
60 min.	10.35	8 X 8	8	8	8	8	0
50 "	10.25	8 X 10	10	10	10	10	0
40 "	10.15	9 X 9	10	10	10	0	0
37 "	10.12	8 X 8	9	9	5	1	1
37 "	10.12	7 X 7	7	7	2	1	1
20 "	9.45	8 X 10	8	4	3	3	0
20 "	10.16		6 X 7	7	3	1	0
15 "	10.11		6 X 7	7	6	5	5
15 "	10.11		7 X 8	8	6	3	3

c. Geotropic stimulation after heliotropic stimulation.

Seedlings were subjected to atimulation from an 8 cp. light 1 meter distant, for 60 minutes, or until they had all responded. They were then placed horizontally in the dark with the tips pointing downward. At the same time plants not previously heliotropically stimulated were also laid horizontally in the dark. In 45 minutes the tips of the control plants were all pointing toward the light, while the decrease in the angles of those which had first been heliotropically stimulated did not take place for 1/2 to 2 hours. Different lengths of exposure were tested and the following results were obtained at a temperature of 25° C.

60 min. exposure gave a retardation of 80 min.
50 " " " " 80 "
40 " " " " 75 "
30 " " " " 25 "
20 " " " " 5 "
10 " " " " 3 "

These experiments show that previous heliotropic stimulation interferes with the entrance of geotropic curvature when an 8 cp. light is used, and thus accord with those performed by Czapek. The following results are those obtained by the use of the 4 cp.

light screened with 3 ground glass plates. This intensity of light as shown above, gives for heliotropism the same presentation period as for geotropism, namely, 12 minutes. Constant use was also made of the klinostat.

The pots were placed on the wheel with the rows of seedlings at right angles to the rays of light and the klinostat was set in action. In 60 minutes 36 out of 38 plants were turned toward the light. They were then taken from the klinostat and laid horizontally in the dark with other seedlings which had not been heliotropically stimulated. 24 out of 25 of the control seedlings had responded in 60 minutes, while there was no decrease in the angles of those previously heliotropically stimulated for 80 to 90 minutes.

This shows that even with the light of such an intensity there is a retardation in the entrance of geotropic response.

CONCLUSIONS.

1. The geotropic presentation period of Avena sativa, with the growth conditions employed and at a temperature of 24°, is 12 minutes.

2. The heliotropic presentation period for Avena sativa subjected to a light equal to 12.6 Hefnerlamps, is not more than 1/4 minute.

3. A heliotropic presentation period of 12 minutes may be obtained by the use of a light equal to 1.4 Hefnerlamps.

4. Seedlings respond to stimulation without regard to former opposing stimulation of the same kind.

5. Primary geotropic stimulation does not effect subsequent heliotropic response.

6. Previous heliotropic stimulation retards the entrance of the response to geotropic stimulation.

This retardation may be very much decreased by lowering the intensity of the light until the presentation periods are of equal length. It is not, however, entirely eliminated.

Whether this retardation is due to the fact that the heliotropic excitation decreases the sensibility of the plant for geotropic stimuli, or whether the action of gravity is not strong enough to overcome the heliotropic response is still to be demonstrated. This may be determined in three ways. First, by finding the geotropic presentation period for a plant heliotropically curved. Secondly, by subjecting a plant to geotropic stimulus which has been heliotropically curved, and then straightened on the klinostat by autotropism. Thirdly, by subjecting the plant to centrifugal force sufficient to overcome retardation.

These experiments I hope to perform in the near future.

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